Large mammalian herbivores in tropical forests with either hindgut- or forestomach-fermentation

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Abstract

Compiled and discussed data on the distribution of both hindgut- and forestomach-fermenting herbivores in the canopy and on the floor of tropical forests in the Neotropical, Ethiopian, Oriental, and Australian regions. Lists of species were compiled from the literature and grouped according to differentiations of the hindgut and the forestomach. The following observations were made:
1. The Neotropical region houses only few forestomach-fermenters, however, hindgut-fermenters, in large quantities, live in this region;
2. Food of intermediate quality is preferred by the pooled hindgut- and forestomach-fermenters;
3. Hindgut-fermenters prefer a more nutritious food than do forestomach-fermenters;
4. Inhabitants of the canopy of the forest prefer a higher quality food than do mammals feeding on the forest floor;
5. Hindgut-fermenters feed predominantly in the canopy and forestomach-fermenters on the forest floor;
6. Detoxification of secondary plant subtances in the food of herbivores is of ecological advantage and a few forestomach-fermenting inhabitants of the canopy apply this strategy. The findings demonstrate a remarkable interrelationship between digestion strategies and distribution of herbivores.

Introduction

During recent years the comparative and functional anatomy of the digestive tract, mainly the stomach, of herbivorous mammals has been intensively studied (Langer 1984a, b, 1985a). The term "herbivore" is used according to Dubost (1979) and includes all mammals that feed on whole plants or parts of plants (grass, leaves, petioles, stems, seeds, fruits, etc.). This means that the term "herbivore" is used in a very broad sense in this paper. Reference will also be made to those mammals consuming food composed of not only plant, but also of animal origin. This group will be referred to as "omnivores".

Two different sites of microbial digestion have to be distinguished (Fig. 1). Enzymes can be produced by microbes (mainly bacteria) that are housed in the hindgut or in the forestomach. Fermentation in the hindgut is probably the phylogenetically older of the two types of strategies applied in microbial digestion in herbivores (Hume and Warner 1980; Langer 1985a). Plant material is degraded by microbial enzymes ("alloenzymatic digestion") in the two main regions of the large intestine, namely, the caecum and the colon (Fig. 1). This hindgut zone, where especially carbohydrates are digested, lies far distal to the stomach where digestion of proteins takes place in an acid environment with the help of digestive enzymes produced by the mammal itself ("autoenzymatic digestion").

In the so-called forestomach-fermenters alloenzymatic digestion might also take place in the hindgut, but the important point is that a specialized gastric region, the forestomach, houses symbionts that are responsible for alloenzymatic digestion. Metabolic products of microbial activity can be absorbed and the bodies of microbes can be autoenzymatically digested in the hindstomach and small intestine that follow fermentation in the forestomach. Microbial activity in the gastrointestinal tract, which degrades the structural
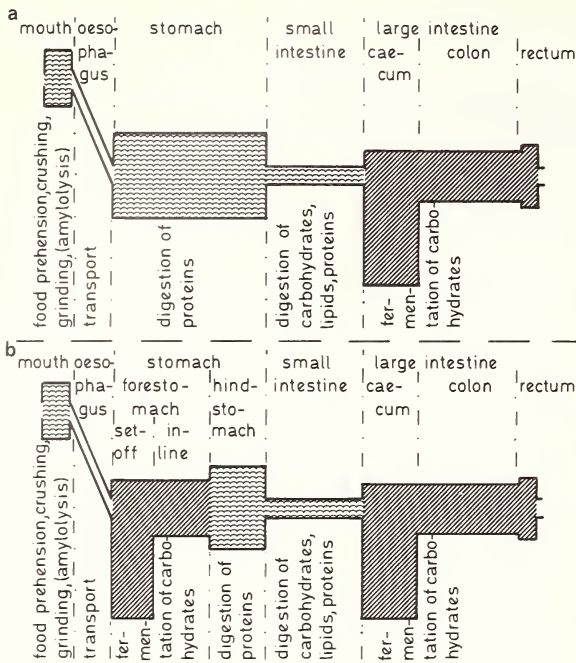
Fig. 1. This illustration compares hindgut-fermenters (a) with fore-stomach-fermenters (b). Regions with autoenzymatic digestion, i. e., withouth structurally important microbial activity, are marked by waves. Regions with alloenzymatic digestion, i. e., with microbial symbionts, are marked by oblique lines. a: Only the large intestine is marked as a zone with alloenzymatic digestion: hindgut-fermenters; b: In addition to the large intestine a part of the stomach (forestomach) is marked as an alloenzymatically digesting zone. Between the fore-stomach and the large intestine the hindstomach and the small intestine are characterized as auto-enzymatic regions: forestomach-fermenters

carbohydrates of the plant cell wall and makes available considerable amounts of microbial protein, opened new nutritional niches. Plant material of higher, but also of very low quality could be used by the mammal. Food of extremely low quality can at least periodically be found in many grasslands of the world.

In previous studies the importance of the development of grasses and grasslands in relation to the evolution of Artiodactyla (LANGER 1974) and Macropodidae (LANGER 1979, 1980) was emphasized. Many grasslands of the world are characterized by considerable fluctuations in food quality and quantity (GWYNNE and BELL 1968; BELL 1970, 1971; HARRINGTON 1981; PALADINES 1984) and forestomach-fermenting herbivores are well adapted to fluctuations in the amount and in quality of food. It has to be asked whether biotopes other than grasslands are stable systems and what role is played by forestomach- and hindgut-fermenting mammals in other biotopes.

Tropical forests do not show the constancy in all climatic parameters as is often attributed to them, especially changes in intensity of precipitation over the course of the year can be observed. Related to this, the quantity and quality of plant material fluctuates in these forests. It is characteristic that the changes in different stages of plant development are not synchronized with each other (WALTER and BRECKLE 1984). Nonseasonal flower, fruit and leaf cycles can be observed (RICHARDS 1973) and variations in abundance, nature, and availability of food are quite marked in "this seemingly uniform environment" (BOURLIERE 1973).

Considering these variable conditions, it seems a promising approach to investigate the distribution of herbivores (heavier than 3 kg) in tropical forests. These animals apply different digestive strategies and eat different types of food, from a diet mixed of animal and plant material to grass. The Neotropical, Ethiopian, Oriental, and Australian zoogeo-graphical regions will be discussed in this article. Emphasis will not be on ecological aspects, but on the problem how different strategies of digestion, namely, hindgut- and forestomach-fermentation, are applied by mammals in tropical forests.

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CONSIDERED   SPECIES
Infraclass: METATHERIA
   Order: Polyprotodonta (NOT considered!)
   Order: Paucituberculata (NOT considered!)
   Order: DIPROTODONTA
      Families (n = 6) except Macropodidae
                  35 species considered............        HF
      Family: MACROPODIDAE
                  29 species considered..........................          FF
Infraclass: EUTHERIA
   Order: PRIMATES
    Suborder: Prosimiae (NOT considered!)
    Suborder: SIMIAE
       Families (n = 6) except Colobidae
                  104 species considered...........       HF
       Family: COLOBIDAE
                  24 species considered..........................         FF
   Order: EDENTATA
       Family: BRADYPODIDAE
                  5 species considered............
                                                          FF
   Order: Lagomorpha (NOT considered!)
   Order: Rodentia (NOT considered!)
   Order: PROBOSCIDEA
                  2 species considered..........................
                                                              HF
   Order: HYRACOIDEA
                  3 species considered............   HF
   Order: PERISSODACTYLA
                  7 species considered..........................    HF
   Order: ARTIODACTYLA
    HINDGUT-FERMENTERS:
       Family: SUIDAE
                  6 species considered............         HF
    FORESTOMACH-FERMENTERS:
       Family: SUIDAE
                  1 species considered..........................      FF
       Family: TAYASSUIDAE
                  2 species considered............      FF
       Family: HIPPOPOTAMIDAE
                  1 species considered..........................      FF
    Suborder: RUMINANTIA
                  45 species considered............      F F
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Fig. 2. In a tabulated form those mammalian families that are considered in this paper, are presented. The different taxa are identified as hindgut- (HF) or forestomach-fermenters (FF). Each family is identified by outlines of one of its species and characterized by different shading. All representatives of the artiodactylan Nonruminantia are characterized by vertical lines. Since one species of the Suidae, namely, *Babyrousa babyrussa*, is, most probably, a forestomach-fermenter, the suids are listed twice. When a taxonomic group is not considered in this work because of lack of sufficient data on nutritional characteristics or because of average body weight that lies below 3 kg, this group has been listed, but is clearly marked as "NOT considered"

Material and methods

The information on gastric anatomy of herbivores is from the author's own investigations, that on the anatomy of the hindgut is from many different sources in the literature. Information on hindgut and forestomach anatomy represents the morphological basis to attribute mammalian taxa to two different digestion strategies, namely, hindgut- and forestomach-fermenters. The data on distribution, body size and food are from the literature. The following sources were used in relation to the distribution of herbivores in tropical forests: DAVEY (1976), DORST and DANDELOT (1973), GRZIMEK (1970/79), HALTENORTH (1958, 1963), LANGER (1974a, 1985a), WETZEL (1982).

Fig. 2 is a compilation of the mammalian families from which the species living in tropical forests were chosen for consideration in this paper. Some mammalian orders are not listed (e.g., Chiroptera), others are listed, but "NOT considered" in the following. This has been done because these orders consist of species that are predominantly smaller than 3 kg or are omnivores consuming a considerable amount of animal food (e.g., many rodents, LANDRY 1970). Especially for the smaller mammalian inhabitants of tropical forests, data on the type of food were not sufficiently available to the present author. It has to be emphasized that those groups that will not be considered in the following can nevertheless be of very great ecological importance (e.g., Chiroptera as pollinators of tropical trees)!

The body weight of mammals has been carefully compiled by EISENBERG (1981), who presents data not only for eutherians, but also for marsupials. However, the number of data for the marsupial order Diprotodonta (sensu KIRSCH 1977) in the table by EISENBERG (1981) is limited and body weights for different diprotodonts were compiled from original papers, namely: DAWSON and BENNETT (1978), DEGABRIELE and DAWSON (1979), DELLOW et al. (1983), GANSLOSSER (1977), HARROP and DEGABRIELE (1976), HUME (1977), MAYNES (1976), NICOL (1978), RÜBSAMEN et al. (1983), and SHAW and ROSE (1979).

The data on the type of food of tropical mammals have mainly been compiled by LANGER (1985a). As these data are from many different sources, reference should be made to the compilatory tables in that publication. From the descriptions of the type of food, mammals were classified into six groups of "herbivory rating". This rating was first described in essence by EISENBERG (1978) and has been extended by LANGER (1984a, 1985a, b).
1. Omnivores with a considerable amount of animal material in their food;
2. Frugivores, very little animal material in the food;
3. Mammals that eat a mixture of fruits, bulbs, and tubers, combined with some herbs;
4. Species that eat fresh leaves with only few seeds;
5. Mammals eating older leaves plus material more difficult to digest, such as grass and twigs;
6. Obligate grazers.

Results

In Fig. 3 data on mean body weight and on mean herbivory rating are compiled. The forestomach-fermenting Nonruminantia (Hippopotamidae and Tayassuidae) are represented by one value, but the Macropodidae are depicted twice; to the left the arboreal ("ar") tree kangaroos of the genus *Dendrolagus* are depicted, to the right the terrestrial ("te") representatives of the Macropodidae can be found.

It can be seen that large herbivores tend to have a higher value of herbivory rating, i.e., they eat a lower quality food (exception: hindgut-fermenting Suidae). It has to be kept in mind that the standard deviation, which is represented by vertical and horizontal bars, is very large in most cases, but the mean body weight of all considered families lies above 3 kg.

Table 1 lists the number of species that are either hindgut- or forestomach-fermenters (A) or have an arboreal or a terrestrial habitat (B). The Neotropical and Ethiopian regions are subdivided into two areas north and south of the equator. Table 2 lists the mean values of herbivory rating in hindgut- and forestomach-fermenters (A) and in canopy- and forest floor-dwellers (B) in each of the zoogeographical regions, as well as arboreal and terrestrial species (C) according to digestive strategy in each of the six regions.

In Fig. 4 the distribution of large hindgut- and forestomach-fermenters in tropical forests is compiled according to different criteria. For each of the forest areas in the northern and southern Neotropical and Ethiopian regions and for the Oriental as well as for the Australian regions a diagram consisting of four parts has been compiled. In each of
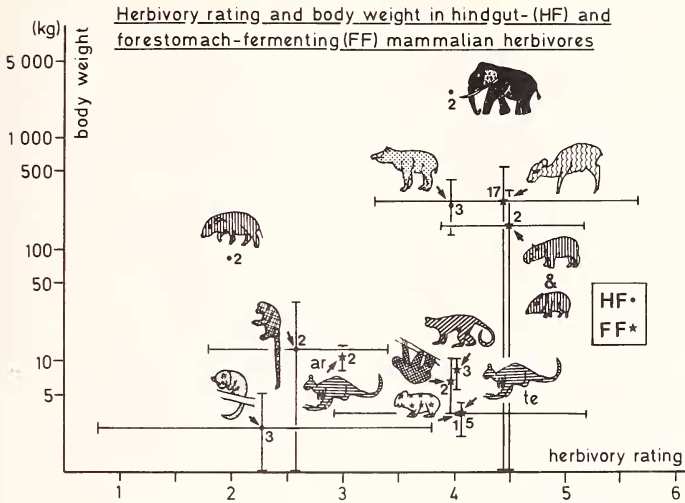
Fig. 3. This illustration gives the means of body weight and herbivory rating for hindgut-fermenters (dots) and forestomach-fermenters (asterisks), together with standard deviations. The means are identified with the symbols introduced in Fig. 2. The numbers near the dots or asterisks indicate the number of species for which data were available for this compilation. The following species are considered:

Arboreal and hindgut-fermenting DIPROTODONTA: *Vombatus ursinus* (only of peripheral importance in tropical forests), *Trichosurus vulpecula, Petaurus breviceps.*

Terrestrial and forestomach-fermenting MACROPODIDAE: *Bettongia tropica, Aepyprymnus rufescens, Thylogale thetis, Macropus parma, Lagorchestes conspicillatus.*

Arboreal and forestomach-fermenting MACROPODIDAE: *Dendrolagus dorianus, D. inustus.*

Terrestrial and hindgut-fermenting PERISSODACTYLA: *Tapirus terrestris, T. bairdi, T. indicus.*

Terrestrial and hindgut-fermenting NONRUMINANTIA: *Sus scrofa, Potamochoerus porcus.*

Terrestrial and forestomach-fermenting NONRUMINANTIA: *Tayassu tajacu, Choeropsis liberiensis.*

Terrestrial and forestomach-fermenting RUMINANTIA: 17 species of the following genera: *Tragulus, Moschus, Muntiacus, Cervus, Odocoileus, Mazama, Pudu, Okapia, Tragelaphus, Taurotragus, Bubalus, Syncerus, Bos, Capricornis.*

Arboreal and hindgut-fermenting PRIMATES (SIMIAE): 20 species of the following genera: *Pithecia, Saimiri, Cebus, Aluatta, Lagothrix, Ateles, Callimicio, Callithrix, Cebuella, Leontideus, Sanguinus, Macaca, Hylobates, Symphalangus, Pongo, Gorilla, Pan.*

Arboreal and forestomach-fermenting COLOBIDAE: *Presbytis obscurus, Nasalis larvatus, Colobus badius.*

Arboreal and forestomach-fermenting EDENTATA: *Bradypus tridactylus, Choelopus hoffmanni.*

Arboreal and hindgut-fermenting HYRACOIDEA: *Dendrohyrax spec.*

Terrestrial and hindgut-fermenting ELEPHANTIDAE: *Loxodonta africana, Elephas maximus*

the diagrams the columns above the horizontal line represent arboreal forms, below the horizontal line terrestrial species are considered. To the left of the vertical line hindgut-fermenters and to the right forestomach-fermenters are represented. It can be seen that only very few forestomach-fermenting herbivores – all of them representatives of the Ruminantia – consume a food of extremely low quality, which means that they can be called obligate grazers. This fact is not at all astonishing because of an almost complete absence of grasses in tropical forests. Only on clearings – either natural (fallen trees) or man-made – can small areas covered with grass be found. These areas are temporal differentiations, returning to forest very rapidly (RATTRAY 1960).

The illustration simplifies the complex relation between types of food, taxonomy, habitat, and biogeography, but it shows trends in the distribution of mammals in tropical forests. With respect to comparative considerations the following observations can be made in Fig. 4:

Table 1

Number of hindgut- and forestomach-fermenters (A) as well as arboreal and terrestrial
herbivores (B) in six zoogeographical regions

Percentages of total are given in brackets

| | Neotropical | | Ethiopian | | Oriental | Australian |
	north	south	north	south		
total	51	62	54	27	65	62
A. hindgut-ferm.	42 (82%)	53 (85%)	28 (52%)	13 (48%)	28 (43%)	33 (53%)
forestom.-ferm.	9 (18%)	9 (15%)	26 (48%)	14 (52%)	37 (57%)	29 (47%)
B. arboreal	43 (84%)	57 (92%)	28 (52%)	12 (44%)	39 (60%)	40 (65%)
terrestrial	8 (16%)	5 (8%)	26 (48%)	15 (56%)	26 (40%)	22 (35%)

Table 2

Mean herbivory rating (HR) in hindgut- and forestomach-fermenters (A) and inhabitants of the
canopy and floor of the tropical forest (B), as well as numbers of arboreal and terrestrial
herbivores with the two digestive strategies (C)

| | | | Neotropical | | Ethiopian | | Oriental | Australian | total |
			north	south	north	south			
A. mean HR	hindgut– ferment.		2.2±1.0 (n=42)	2.2±0.8 (n=53)	3.5±0.9 (n=28)	3.5±1.1 (n=13)	3.3±1.2 (n=28)	2.7±1.2 (n=33)	2.7±1.1 (n=197)[1]
	foresto.- ferment.		4.1±0.3 (n=9)	3.9±0.8 (n=9)	4.1±0.7 (n=26)	4.3±0.6 (n=14)	4.5±1.3 (n=37)	3.9±0.8 (n=29)	4.1±0.7 (n=124)[1]
B. mean HR	forest canopy		2.2±1.0 (n=43)	2.3±0.9 (n=57)	3.6±0.8 (n=29)	3.5±0.9 (n=12)	3.6±0.8 (n=39)	2.6±1.0 (n=40)	2.8±1.1 (n=220)[1]
	forest floor		4.1±0.4 (n=8)	3.8±1.1 (n=5)	4.0±0.8 (n=25)	4.2±0.9 (n=15)	3.9±1.4 (n=26)	4.2±0.8 (n=22)	4.1±1.0 (n=101)[1]
C. arboreal	hindg.-f.		39	53	25	10	19	32	29.7±15.2
	fo.st.-f.		4	4	3	2	20	8	6.8±6.8
terrestrial	hindg.-f.		3	0	3	3	9	1	3.8±3.0
	fo.st.-f.		5	5	23	12	17	21	13.8±7.8

[1] When a species lives in more than one zoogeographical region, it appears here more than once.
The sum of these numbers is therefore not indentical with the sum of all considered species as
listed in Fig. 2!

1. In the Ethiopian and Oriental regions the majority of forestomach-fermenters is
   represented by the Ruminantia, in Australia by the Macropodidae. Only few fore-
   stomach-fermenters inhabit the Neotropical region.
2. Most hindgut- and forestomach-fermenters prefer food of intermediate quality, i.e.,
   most are compiled under the classes 3 and 4 of herbivory rating.
3. Hindgut-fermenters in tropical forests tend to live on food of higher quality than
   forestomach-fermenters.

4. Inhabitants of the forest canopy tend to eat a higher quality food than inhabitants of the forest floor.
5. Hindgut-fermenters feed predominantly in the forest canopy, forestomach-fermenters prefer the forest floor.
6. The exception to the last statement is represented by the Bradypodidae, Colobidae, and tree kangaroos, which are forestomach-fermenting inhabitants of the forest canopy.

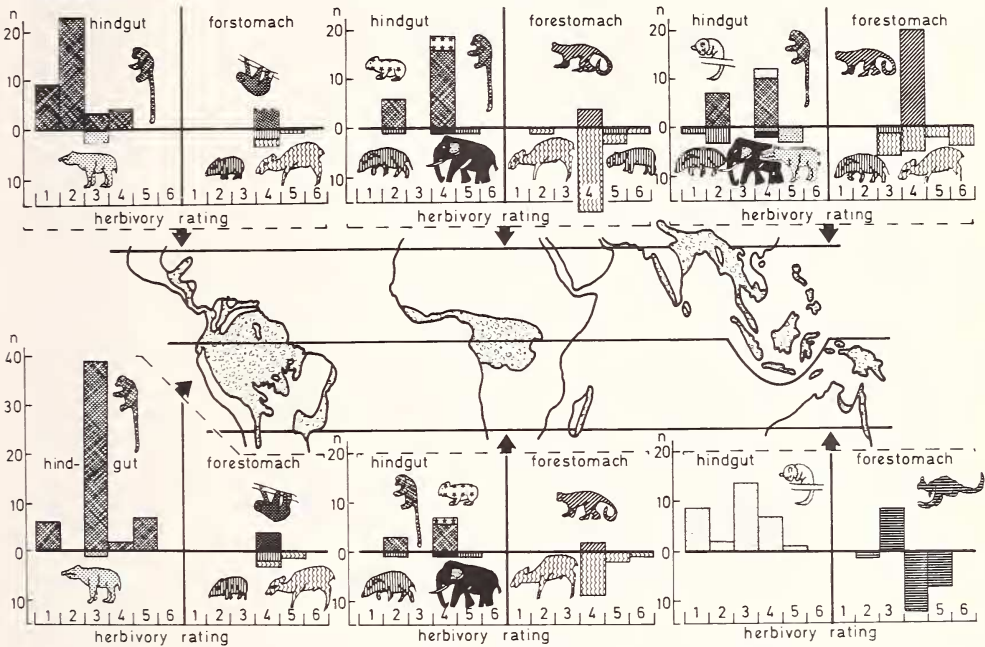The distribution of larger hindgut- and forestomach-fermenting herbivores in tropical forests

Fig. 4. Diagrams are given for tropical forests (stippled on the map) in six zoogeographical regions. The symbols and the columns that indicate the species inhabiting the respective regions, are identical with those introduced in Fig. 2. The left part of each diagram refers to hindgut-fermenters, the right part to forestomach-fermenters. Above the horizontal lines the columns represent inhabitants of the forest canopy and below these lines the forest-floor dwellers are found. Both in hindgut- and forestomach-fermenters the taxa are grouped according to their food, which is characterized on the horizontal axis by values (1 to 6) of herbivory rating. The vertical axis refers to the number of species

Discussion

Tropical forests cover 11945500 square km (BROWN and LUGO 1984), which equals approximately 8 % of the total land surface of the world (151153000 square km). According to WHITTAKER and LIKENS (1975), 1025 giga-tons of total biomass (dry matter) can be found in the tropical forests (rain plus seasonal forests). This represents approximately 56 % of the total biomass on the continents of the world (1837 giga-tons, WHITTAKER and LIKES 1975). In a central Amazonian rain forest approximately 2.5 % of the total above-ground phytomass is represented by leaves of dicotyledonous trees and palms (KLINGE et al. 1975). About 560 g/square metre/year of foliage (dry matter) are produced in tropical forests (Mean of 12 areas; range from 150 to 1200 g/square metre/ year, CANNELL 1982). According to WHITTAKER and LIKENS (1975) the mean net primary production of dry plant matter (total plants considered) in tropical rain forests and tropical

seasonal forests is about 1900 g/square metre/year. This would mean that the annual production of foliage represents about 30 % of the whole annual plant production. As only 2.5 % of the total plant matter is represented by foliage, the turnover has to be very high in leaves. Total synthesis taking place in the foliage, which is responsible for the differentia-tion of the material of the whole tree, is not discussed here, but only production of leaf material. It should be mentioned here that the mean production of fruits (dry matter) amounts to 102.5 g/square metres/year (calculated from CANNELL 1982), which is equiva-lent to approximately 5.4 % of the whole annual plant production.

Herbivores that prefer freshly grown plant material concentrate on fruits or leaves. Both plant products follow many different rhythms, the causes of some of which are poorly known. Periods of minimum leaf flush, when only few new leaves are available to herbivores, cannot be predicted. "Vertebrate folivores seem to be limited by the seasonal shortage of new leaves" (results from Barro Colorado Island, Panama, by LEIGH and WINDSOR 1982) and the same is also true for fruits and frugivores (GHIGLIERI 1985). Changes in the chemical constituents of leaves are related to the age of leaves, and quantitative and qualitative chemical changes influence palatability and nutritive value. An explanation for the chemical and nutritional fluctuations can be found in climatic variabil-ity (MCKEY 1979; MCKEY et al. 1981). Data for equatorial weather stations, as listed by RICHTER (1983), show that the mean monthly precipitation can range from 0.1 % to 23.8 % of the mean annual precipitation (Fig. 5). "Rainfall by itself is probably of little importance for a mammal; it acts indirectly through its influence on primary and secondary productivity; . . ." (BOURLIERE 1973). Newly produced leaves "are suited to herbivores, while mature leaves are relatively unsuitable" (OPLER 1978). Tannins and lignins are important chemical and mechanical defensive components of plants (SWAIN 1979), but alkaloids (ROBINSON 1979), saponins (APPLEBAUM and BIRK 1979), or protein-ase inhibitors (RYAN 1979), to mention just a few classes of substances, play a protective role as "secondary plant compounds". These metabolites of the plant have to be coped

Mean monthly precipitation (expressed as % of annual mean) and mean monthly temperature in four tropical locations.
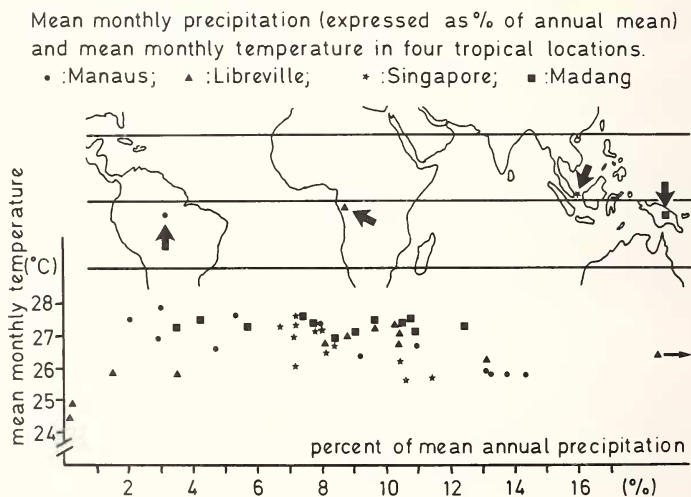
• :Manaus;   ▲ :Libreville;   * :Singapore;   ■ :Madang

Fig. 5. For Manaus, Libreville, Singapore, and Madang the mean monthly temperature is plotted against the percentage of mean annual precipitation in the respective month. The twelve months are not identified, because it is the general tendency and not the detailed analysis that is emphasized here: A small range of mean monthly temperatures (around 27 degrees Celsius) is connected with a considerable range of changes in precipitation, even in the four true equatorial weather stations, of which none is more than 5 degrees north or south of the equator. Other sites that are further away from the equator, show higher amplitudes of mean monthly precipitation between different months. Raw data for this compilation are from RICHTER (1983)

with by the herbivore and there is an evolutionary interrelationship between the synthesis of these "xenobiotics" and their detoxification in the digestive tract of herbivores (HART-MANN 1985).

CRAWLEY (1983) demonstrates that microbial activity detoxifies plant-protection molecules and thus renders many of the secondary plant substances harmless. Especially forestomachs, which have been most intensively studied in the Ruminantia (DOBSON 1967; FREELAND and JANZEN 1974), are important sites where this process of detoxification is very effective, because it takes place very early in the digestive process and autoenzymatic digestion in the subsequent parts of the gastrointestinal tract is not hampered through poisonous substances. This would explain why forestomach-fermenters can be found in the forest canopy of the Neotropical region (Bradypodidae, tree sloths), the Ethiopian and Oriental regions (Colobidae, leaf monkeys), and in the Australian region (tree kangaroos).

Why can forestomach-fermenters cope with a food of low quality? The reason for this lies, most probably, in the position of the site of alloenzymatic digestion. Products of microbial activity, mainly short-chained fatty acids, can be absorbed through the fore-stomach wall and the cell bodies of microbes are autoenzymatically digested in the hindstomach and small intestine (waves in Fig. 1b). When microbial activity takes place in the hindgut (Fig. 1a), the supply of energy, trace elements, and vitamins at this site of alloenzymatic digestion is not very effective (PLAUT 1984). According to SCHMIDT et al. (1982), Bacterial protein produced in the hindgut of the horse is completely evacuated, but amino acids and short-chained fatty acids as products of microbial metabolism are absorbed through the wall of the large intestine (GEYER and DREPPER 1973). Hindgut-fermenters eat a food of higher quality and can afford some loss of microbial protein, which represents a considerable source of energy.

In the tropical forests the total number of species per zoogeographical region can range from 27 species to 65 species (Table 1). There is considerable difference between the two South American regions and the four other areas in relation to digestive strategy as well as distribution in aboral or terrestrial habitats: In the Neotropical region the number of arboreal hindgut-fermenters within the considered groups is much higher than in the Ethiopian, Oriental, and Australian zones. The relative number of terrestrial forestomach-fermenters is small in South America. Is this the effect of radical Quarternary extinction of this group of herbivores or the effect of the long isolation of the continent with separate evolutionary diversifications?

Although it will never be possible to reconstruct internal "soft" organs of extinct species, it seems at least probable that the giant ground sloths that have been clearly identified since the early Oligocene (37 million years ago; SIMPSON 1980) in South America were forestomach-fermenters. The two recent genera with a total of five species of Bradypodidae (tree sloths) can still be found in the tropical forests of that continent (WETZEL 1982). They have a very complicated and voluminous forestomach region (LANGER 1985a) and probably evolved from the Megalonychidae or Megatheriidae (SIMP-SON 1980), both families of the ground sloths. The ground sloths are believed to have been grazers and browsers in relatively open habitats (SIMPSON 1980). 12 genera (MARTIN and GUILDAY 1967) or 19 genera (ANDERSON 1984) of ground sloths have become extinct during the Pleistocene. On the other hand, nothing can be said about the anatomy of the gastrointestinal tract in other herbivores that were primitive inhabitants of South America, such as the Lithopterna, Notoungulata, Astrapotheria, and Pyrotheria (SIMPSON 1969; WEBB and MARSHALL 1982).

At the transition from Eocene to Oligocene (about 37 million years before present, WEBB and MARSHALL 1982) primates and caviomorph rodents, which were certainly hindgut-fermenters as their contemporary descendants are, immigrated into what is now the Neotropical region. Geologically quite recently, during the transition from Pliocene to

Pleistocene (approximately 2 million years ago), hindgut-fermenting rodents, but also hindgut-fermenting tapirs, equids, and mastodonts and forestomach-fermenting Artiodactyla, such as Cervidae, Camelidae, and Tayassuidae, immigrated into South America (THENIUS 1972; MARSHALL et al 1982). It has to be assumed that larger forestomach-fermenters never played a considerable role in South America.

In the Ethiopian, Oriental, and Australian regions hindgut- und forestomach-fermenters each represent about 50 % the considered herbivores (Table 1A). This is very remarkable since this approximate equilibrium of representatives with the two digestive strategies cannot only be found in Eutherians in the northern and southern Ethiopian as well as in the Oriental regions, but also in the diprotodont marsupials of the tropical Australian region. It is assumed that the equilibrium of both digestive strategies is connected with a balanced or stable occupation of available ecological niches. Most niches are settled; to render food material into absorbable molecules, hindgut and forestomach are engaged in microbial alloenzymatic digestion.

In the tropical forests with the exception of the Neotropical one, the mean number of arboreal herbivores only slightly exceeds (55 %) that of terrestrial species (45 %) (Table 1B). It is not yet possible to explain the low absolute number of larger terrestrial herbivores in South America. One theory, which is still very controversially debated, is that of prehistoric overkill by human hunting (discussion in MARTIN and WRIGHT 1967; REMMERT 1982; MARTIN and KLEIN 1984), but it is not known whether this overkill played an important role in tropical forests.

Food characteristics in relation to the distribution of herbivores are to be considered in the following. The comparison of the six diagrams in Fig. 4 gives the impression that the majority of herbivores (hindgut- and forestomach-fermenters pooled) prefer a food of intermediate quality, but hindgut-fermenters tend to a food of better quality than do forestomach-fermenters. This impression is corroborated when the total means (Table 2A) of herbivory rating (HR) in all six biogeographic regions of hindgut-fermenters (HR = 2.7) and forestomach-fermenters (HR = 4.1) are considered. This difference in tendency – hindgut-fermenters often eat food of better quality than do forestomach-fermenters – can be observed in all six zoogeographical regions; this was also identified by CASE (1979). Both digestive strategies demonstrate their functional option with different qualities of food. As only 5.4 % of whole annual plant production (dry matter) is represented by fruits, but 30 % by foliage (see above), a high percentage of the produced fruits is eaten by frugivores, but the amount of foliage mass produced is so large that only a relatively small amount of the produced leaves is eaten by folivores.

A relation between ingestion of a food of better quality (low value of herbivory rating) in animals of in the forest canopy, on the one hand, and the ingestion of a low quality food on the forest floor, on the other hand, can be seen in Table 2B and becomes visible in the six diagrams of Fig. 4. Although the productivity of fruits is much smaller than that of leaves, the forest canopy dwellers preferentially select them (GHIGLIERI 1985) and thereby obtain a lower mean value of herbivory rating. These mammals can be called "concentrate selectors" according to HOFMANN (1973) and HOFMANN and STEWART (1972). On the other hand, it should not be forgotten that many fruits, as well as older leaves, fall down so that a considerable range in food quality can also be obtained on the floor of tropical forests (JANZEN 1970). For example, white lipped peccaries *(Tayassu peccari)* rely on fallen fruits when they are available (KILTIE 1981a, b).

The majority of arboreal species is represented by primates (Fig. 4), in Australia diprotodont Marsupialia are the occupants of this niche (Polyprotodonta and Paucituberculata are not considered in this paper). The inhabitants of the forest floor are represented in the Ethiopian and the Oriental regions by the Ruminantia with the highest number of species.

The forest canopy ("arboreal" in Table 2C) is inhabited by an average of about 30

hindgut-fermenters, but only by seven forestomach-fermenters. On the other hand, only about four hindgut-fermenters, but a mean of about 14 forestomach-fermenters live on the forest floor. Also in Fig. 4 this distribution of both digestive strategies is visible, most clearly in the Ethiopian, Oriental, and Australian regions.

Why do hindgut-fermenters inhabit and feed predominantly in the canopy and fore-stomach-fermenters on the forest floor? It has been shown by a few authors who determined the wet weight of the combined fermentation chambers (hindgut and fore-stomach) that this weight increases approximately linearly with body weight, which means that there is an isometric relationship between both parameters and no considerable difference between hindgut- and forestomach-fermenters (PARRA 1978; VAN SOEST 1982; DEMMENT 1983; DEMMENT and VAN SOEST 1983). This relationship indicates that hindgut-fermenters do not prefer the canopy because this digestion strategy is related with a lower weight of digesta in the gastrointestinal tract. However, the hindgut-fermenters prefer a better quality food (Table 2A), which they can digest autoenzymatically to a high extent. In this situation only small amounts of microbial metabolites are necessary to fulfill the mammal's needs of nutrients. A food of better quality is available in the canopy than on the floor of the forest.

A food of high quality does not require a long retention time to be effectively digested. The hindgut generally retains digesta for a shorter time than does the forestomach (WARNER 1981). Food is quickly digested in hindgut-fermenters, which means that readily absorbable substances are removed and after a relatively short time the remains are voided. Those nutrients that can be made available by autoenzymatic digestion are used and the microbial metabolites play a less important role. Periodical decreases in food quality can be coped with by an increase in the rate of passage of digesta (JANIS 1976; LANGER 1984a), which is only possible when the amount of food does not fluctuate substantially. In the forest canopy the quantity of available food does not vary as greatly as the quality. This whole complex of parameters is the reason for the wider distribution of hindgut-fermenters in the forest canopy than on the forest floor.

On the forest floor the application of the strategy of forestomach-fermentation is appropriate because the fall of fruits and leaves makes this zone, which is relatively poor in fresh plant material, suffer from more intensive fluctuations in the quantity and quality of available food than the canopy. It has been discussed elsewhere that forestomach-fermenters are well adapted to fluctuations in food quality and quantity (LANGER 1984a). In the forestomach-fermenter the products of alloenzymatic digestion, namely, the micro-bial metabolites, but also the microbial cells, are used by the mammalian host to a higher degree than in hindgut-fermenters.

The reader might now remember the sixth observation mentioned under "Results", namely, that Bradypodidae (tree sloths), Colobidae (leaf monkeys) and tree kangaroos, which are all forestomach-fermenters, live and feed in the forest canopy (Fig. 4). Here another aspect of nutrition has to be considered: The climatic fluctuation influences the chemical composition of plant materials, especially leaves. It has already been mentioned above that forestomach-fermenters are able to detoxify secondary plant compounds relatively early in the gastrointestinal tract and thus render a food harmless, which is rich in these substances when ingested. This is the case in the above-mentioned forestomach-fermenting arboreal folivore living in the Neotropical, Ethiopian, Oriental, and Australian biogeographic regions. It has to be emphasized that the ability to decompose secondary plant components in the forestomach has only been proven in the Colobidae (MCKEY et al. 1981), but is quite probable in tree kangaroos, as well as in Bradypodidae. Species from this latter mammalian family have been shown to select against mature leaves that were relatively indigestible (MONTGOMERY and SUNQUIST 1978), but it has to be assumed that one of the reasons why the forestomach-fermenting tree sloths inhabit the forest canopy is their ability to detoxify secondary plant compounds in their forestomach.

The overview in Fig. 4 allows us to subdivide the species belonging to those families compiled in Fig. 2 into four general ecological groups, which can be characterized and exemplified as follows:

a. Arboreal hindgut-fermenting frugivores and browsers: Primates (other than colobids) (Neotropical, Ethiopian, Oriental); tree hyraxes (Hyracoidea) (Ethiopian); Diprotodonta (other than kangaroos) (Oriental and Australian).

b. Arboreal forestomach-fermenting frugivores and folivores: Bradypodidae (Neotropical); Colobidae (Ethiopian, Oriental); tree kangaroos (Macropodidae) (Australian).

c. Terrestrial hindgut-fermenting "intermediate feeders": Perissodactyla (Neotropical, Oriental); Nonruminantia (Ethiopian, Oriental); Proboscidea (Ethiopian, Oriental). This ecological group does not seem to be present in the Australian region!

d. Terrestrial forestomach-fermenting "intermediate or bulk and roughage feeders": Tayassuidae (Neotropical); Ruminantia (Neotropical, Ethiopian, Oriental); Nonruminantia, namely, *Choeropsis liberiensis* (Ethiopian) and *Babyrousa babyrussa* (Oriental); Macropodidae (some), e.g., species of the genera *Aepyprymnus, Thylogale, Macropus* (some) (SANSON 1978) (Australian).

Acknowledgements

Zusammenfassung

Größere herbivore Säuger in tropischen Wäldern als Enddarm- oder Vormagenfermentierer

In dieser Studie wird die Verteilung von Enddarm- und Vormagen-fermentierenden herbivoren Säugern mit einem Durchschnittskörpergewicht von mehr als drei kg, die im Kronenbereich und auf dem Boden tropischer Wälder der Neotropis, Äthiopis, Orientalis und Australis leben, diskutiert. Vormagenfermentierer werden vornehmlich durch Ruminantia und Macropodidae repräsentiert, Enddarmfermentierer durch Primaten und diprotodonte Beuteltiere (außer Macropodidae). Alle anderen Säugetiergruppen spielen nur eine untergeordnete Rolle in bezug auf die Artenzahl. Folgende Beobachtungen konnten gemacht werden:

1. In der Neotropis treten nur sehr wenige Vormagenfermentierer auf. Es wird angenommen, daß diese Verdauungsstrategie nie eine bedeutende Rolle in diesem Gebiet spielte. Nur die bodenlebenden Riesenfaultiere dürften diese Strategie angewandt haben. Die heutigen bodenbewohnenden Vormagenfermentierer sind erst relativ rezente Einwanderer.
2. Nahrung mittelmäßiger Qualität wird besonders häufig gefressen.
3. Enddarmfermentierer ziehen ein Futter höherer Qualität vor, als es Vormagenfermentierer tun. Es ist möglich, daß die Lage weit aboral des Fermentationsortes im Enddarm es unmöglich macht, Produkte der alloenzymatischen Verdauung ausreichend zu verwerten.
4. Bewohner der Baumkronen-Schicht ziehen ein Futter höherer Qualität vor, bodenbewohnende Herbivoren des tropischen Waldes kommen mit einem Futter geringerer Qualität aus.
5. Enddarmfermentierer fressen vornehmlich in den Baumkronen und die Vormagenfermentierer, abgesehen von wenigen Ausnahmen, auf dem Boden. Die praktisch gleichbleibende Menge verfügbaren Futters, verbunden mit den Schwankungen der Nahrungsqualität als Ergebnis des variierenden Niederschlages im Laufe des Jahres, erlauben es, diese Baumkronen-Zone mit Enddarmfermentierern zu besiedeln, welche die Passagezeit der Nahrung durch den Verdauungstrakt zu regeln in der Lage sind.
   Die Anwendung der Strategie der Vormagenfermentierung vornehmlich auf dem Boden des Waldes hängt mit der Tatsache zusammen, daß die Nahrungsmenge – nicht nur die Nahrungsqualität – bedeutend in Teilen der tropischen Wälder schwankt.
6. Die Vormagen-fermentierenden Baumkronen bewohnenden Blattfresser, wie sie durch die Bradypodidae, Colobidae und Baumkänguruhs repräsentiert werden, sind in der Lage, die sekundären Pflanzenbestandteile mit Hilfe ihrer Vormagenmikroben unschädlich zu machen.

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